ARE SALT MARSH INVASIONS BY THE GRASS *ELYMUS ATHERICUS* A THREAT FOR TWO DOMINANT HALOPHILIC WOLF SPIDERS?

Julien Pétillon[1,2], **Frédéric Ysnel**[1], **Jean-Claude Lefeuvre**[3] and **Alain Canard**[1]: [1] E.R.T. "Biodiversité fonctionnelle et Gestion des territoires", Université de Rennes 1, 263 Av. du Général Leclerc, CS 74205, 35042 Rennes Cedex, France. E-mail: julien.petillon@univ-rennes1.fr; [2] U.M.R. C.N.R.S. "Fonctionnement des Ecosystèmes et Biologie de la Conservation", Université de Rennes 1, 263 Av. du Général Leclerc, CS 74205, 35042 Rennes Cedex, France; [3] Laboratoire d'Évolution des Systèmes Naturels et Modifiés, Muséum National d'Histoire Naturelle, 36 rue Geoffroy Saint Hilaire 75005 Paris, France

ABSTRACT. As a result of the *Elymus athericus* (Poaceae) invasion in the last ten years, a major change in vegetation cover has occurred in salt marshes of the Mont Saint-Michel bay (France). In this study, we investigated if the high conservation value of invaded salt marshes is preserved. Abundances, densities and flood resistance abilities of the dominant halophilic species *Arctosa fulvolineata* (nocturnal lycosid) and *Pardosa purbeckensis* (diurnal lycosid) were compared in both natural and invaded habitats. *Elymus* invasion involved both positive and negative aspects with respect to the conservation value of the salt marshes invaded: the *P. purbeckensis* population was clearly reduced in invaded habitats, whereas *A. fulvolineata* seemed to derive high benefits from the invasion. We supposed that abiotic parameters of the new habitat (mainly vegetation and litter characteristics) affected the two species differently with respect to their aut-ecology and their flood resistance abilities. Furthermore, food resources (estimated by different macrofauna density measurements) were likely to be reduced for *P. purbeckensis* in invaded habitats and unchanged for *A. fulvolineata*. Lastly, we hypothesize that individuals of *P. purbeckensis* are subject to increased interspecific competition (measured as intra-guild densities), whereas spiders from the same guild as *A. fulvolineata* have not increased in invaded habitats, resulting in an unchanged competition level.

Keywords: Conservation value, halophilic species, habitat change, invasive species, food resources

Salt marshes are one of the rarest ecosystems in the world (Lefeuvre et al. 2000), with a linear but fragmented distribution along coasts, therefore representing a high interest in terms of nature conservation (e.g., Gibbs 2000; Bakker et al. 2002). In fact, these ecosystems host a poorly diversified flora and fauna, which possess a low number of species that are threatened directly or indirectly by human activities such as habitat destruction, diffuse soil pollution from adjacent cultivated fields, and overgrazing (Desender & Maelfait 1999; Adam 2002). The high conservation value of these habitats is also due to the high specificity of its fauna, adapted to two main abiotic factors, high soil salinity and regular submergence by seawater. Due to tidal events, natural salt marshes present a specific plant cover (spatial succession from the high to the low marsh) and specific invertebrate communities dominated by some "halophilic arthropods" (Foster & Treherne 1976; Irmler et al. 2002; Pétillon et al. 2004).

In the Mont Saint-Michel bay, France, salt marshes have been invaded by a native species *Elymus athericus* (Link) Kerguélen (Valéry et al. 2004). This high marsh-living grass (Poaceae) started to invade the salt marsh 10 years ago (Bouchard et al. 1995) and now covers some marshes to the mean sea tide level. This progression is characteristic of an invasive species that is common in European salt marshes (Bockelmann & Neuhaus 1999). Nevertheless, the effects of *E. athericus* invasions on the high conservation value of salt marshes remain unknown. Spiders constitute an abundant, diversified and well-known taxonomic group in salt marshes (Fouillet 1986; Desender & Maelfait 1999), including specialist (stenotopic) species, the so-called "hal-

Table 1.—Synthesis of field experiments carried out in the Mont Saint-Michel bay salt marshes ('Ferme Foucault' and 'Vivier-sur-mer' sites).

Parameter	Methodology	Period	Number of replicates
Target species abundances	Pitfall trap (r = 5 cm)	April–November 2002	8
Target species densities	Depletion quadrat (1 m^2)	June–July 2003	32
Target species abundances before and after the tide	Pitfall trap (r = 5 cm)	April 2004	12
Abiotic parameters	WET sensor and manual measurements	July–August 2002	16
Macrofauna densities	Soil cores (r = 5 cm)	October 2003	6
Amphipod densities	Depletion quadrats (1 m^2)	June 2003	4
Total spider densities	Depletion quadrats (0.25 m^2)	June 2002	16

ophilic species" (Hänggi et al. 1995) or "salt marsh resident species" (Pétillon et al. 2004). In Europe, the numerically dominant hunting spiders in salt marsh ecosystems are the rare lycosid species *Pardosa purbeckensis* F.O. Pickard-Cambridge 1895 and *Arctosa fulvolineata* (Lucas 1846) (Fouillet 1986; Baert & Maelfait 1999; Elkaim & Rybarczyck 2000). *Pardosa purbeckensis* will be considered in this study as different from *P. agrestis*, dominant in Central Europe agricultural landscapes (e.g., Samu & Szinetár 2002) and inland salt marshes (e.g., Zulka et al. 1997), mainly because of its morphological characteristics (as described in Locket & Millidge 1951) and its osmoregulatory abilities (Heydemann 1970). *Arctosa fulvolineata* is classified as a nationally endangered species in the United Kingdom (Harvey et al. 2002) and belongs to the "rare species" category in the Ramsar Convention.

The aim of the study was to investigate if the newly created vegetation cover induced by the invasion of *Elymus athericus* still constitutes a suitable habitat for these two species of high conservation value. To explain the potential impact of the invasive plant on spider species habitat preferences, natural and invaded habitats were characterized by abiotic and biotic components. We hypothesized that *Elymus athericus* changed the general microhabitat characteristics and induced 1) an effect on species density, activity density and flooding resistance due to less appropriate abiotic parameters (e.g., salinity or litter depth), 2) a change in the quality and quantity of food resources, and 3) a variation in the predation rate (measured as intra-guild densities) upon the two species *Arctosa fulvolineata* and *Pardosa purbeckensis*.

METHODS

Study sites and field surveys.—The Mont Saint-Michel bay, located between Brittany and Normandy (North West France), is unique in Europe for its tidal amplitude, which reaches 15 meters (the second largest in the world). This exceptional phenomenon results in the extension of salt marshes and mud flats, which together cover 250 km^2. Salt marshes are only submerged during spring tides (i.e. monthly strong tides) and are then inundated during two hours per tide (Lefeuvre et al. 2000). The uppermost parts of the salt-marshes are delimited by dikes and are not submerged during high tides.

Natural stations (dominated by *Atriplex portulacoides*, Chenopodiaceae) and invaded stations (dominated by *Elymus athericus*, Poaceae) were located at the same distance from the dike. Habitat characterization and measurements of spider activity and density were carried out at four stations (two natural and two invaded) located at the 'Ferme Foucault' site' (Normandy, 48°55′N, 1°52′W) whereas experiments on species reactions to flooding were carried out at six stations (three natural and three invaded) located at the 'Vivier-sur-mer' site (Brittany, 48°60′N, 1°78′W).

Spider sampling.—*Spider abundances:* Spiders were sampled with pitfall traps, consisting of polypropylene cups (10 cm diameter, 17 cm deep) set into the ground so that the lips were flush with the soil surface. Ethylene glycol was used as preservative, because of its lack of effects on spider catches

Table 2.—Mean spider activity abundances (number of individuals/day/meter ×10) and mean densities (number of individuals/m^2) in invaded and natural vegetations, and statistical comparisons using ANOVA (Code: n.s. = non significant, * = $P < 0.05$, ** = $P < 0.01$).

	Natural plots	Invaded plots	F-ratio	Code
Spider abundances				
Arctosa fulvolineata	9.31 ± 3.09	9.83 ± 3.15	0.01	n.s.
Pardosa purbeckensis	98.5 ± 23.80	41.72 ± 7.70	5.13	*
Spider densities				
Arctosa fulvolineata	0.03 ± 0.03	0.43 ± 0.12	9.71	**
Pardosa purbeckensis	3.93 ± 1.24	1.37 ± 0.27	4.09	*

(Topping & Luff 1995). Traps were covered with a raised wooden roof to keep out rain. Catches in pitfall traps were related to trapping duration and pitfall perimeter, which calculates an 'activity trapability density' (number of individuals per day and per meter: Sunderland et al. 1995). Four pitfall traps were installed at each station and spaced 10 meters apart, considered as the minimum distance for avoiding interference between traps for spider catches (Topping & Sunderland 1992). Activity trapability density of spiders was followed during the entire period of activity of the two species from April–November 2002 except during high tides (Table 1).

Spider densities: To compare absolute densities of the two lycosids, 1m × 1m plastic quadrats (1 m height) were used. Quadrats were sampled by regular hand catches and pitfall traps (one placed in the middle of the quadrat) until there were no more individuals. Eight spatial replicates were sampled in each vegetation type (i.e. invasive and natural), and this technique was used four times in June and July 2003 (i.e. 32 replicates per vegetation: Table 1).

Effects of flooding: To determine the role of vegetation cover in modifying species ability to resist flooding, spiders were sampled before and after a spring tide (tidal range: 13.35 m) in April 2004 (Table 1). Three natural and three invaded stations were studied at three salt marsh levels ranging from the high to the low marsh (i.e. 50, 150 and 200 meters from the dike). Four pitfall traps per station were activated during three consecutive days before and after the high tide. Catches were completed by hand collecting during activation and collection of pitfall traps for a total of 1.5 hours per station before and after the high tide.

Characterization of natural and invaded habitats.—*Abiotic characteristics:* To characterize plant communities, vegetation was described four times within a radius of 1 m around each pitfall trap (4 replicates per station) at the 'Ferme Foucault' site: litter depth (to the nearest mm) and vegetation height (to the nearest cm). Soil salinity (estimated by pore water electrical conductivity), soil water content and temperature were measured using a W.E.T. Sensor connected to a moisture meter HH2 (Delta-T Devices Ltd., Cambridge, UK) and made with a specific clay soil calibration. All abiotic variables were assessed in summer 2002 (Table 1). Soil temperatures were measured at 11h a.m. to compare this micro-climate parameter between habitats, but not to characterize it along time.

Biotic characteristics: Food resources were estimated by vertical sampling using a soil core (12 cm depth and 10 cm for diameter), except for the very mobile amphipod (see below). Six cores were collected in each habitat (natural or invaded) during October 2003 (Table 1). Cores were then sieved through a 250 μm mesh screen. Because cannibalism and intraguild predation are a general rule in spiders, especially in structurally simple ecosystems (e.g., Schaefer 1974), spider densities were included in total arthropod densities when comparing the food resources between invaded and natural areas. The results do not include an important macrofauna component, the gastropod *Phytia bidentata* because this species is not likely to be consumed by the two lycosid species.

Because the amphipod *Orchestia gammarella* represents one of the more abundant arthropods in west European salt marshes (e.g., Meijer 1980), special attention was paid to

Table 3.—Comparison of mean activity abundances measured by pitfall traps (number of individuals/day/meter; in parentheses: total number of individuals) before and after the high tide in natural and invaded stations, and statistical comparisons using ANOVA (Code: n.s. = non significant, * = $P < 0.05$, ** = $P < 0.01$).

	Species abundances			
	Before the high tide	After the high tide	*F*-ratio	Code
Natural stations				
Arctosa fulvolineata	1.77 ± 0.49 (40)	0.44 ± 0.21 (18)	6.14	*
Pardosa purbeckensis	3.36 ± 1.14 (364)	2.12 ± 0.47 (274)	1.00	n.s.
Invaded stations				
Arctosa fulvolineata	0.97 ± 0.28 (31)	0.80 ± 0.27 (23)	0.21	n.s.
Pardosa purbeckensis	4.69 ± 1.06 (214)	2.03 ± 0.51 (163)	5.04	*

this species. Densities of *O. gammarella* were calculated in natural and invaded habitats using a depletion method. Within each plant community, four 1m^2 quadrats were randomly sampled in June 2003 by hand catches and pitfall traps until there were no more individuals.

To measure nocturnal and diurnal wanderer densities, spider densities were estimated by the quadrat-flotation technique. Homogeneous 0.25 m^2 areas were isolated by iron quadrats (0.5 meter width and 1 meter height) set into the ground to a depth of 0.20 m. All vegetation was removed, stored in sealed bags and analyzed in the laboratory. The spiders remaining within the quadrat were then hand collected on the bare soil until none were visible. A pitfall trap was placed in the middle of the quadrat and left in place until all remaining moving individuals were caught. A last hand collection was also carried out during the time of pitfall trapping. The spider density was calculated by summing individuals of the initial and final hand collections with the catches of both pitfall trap and vegetation samplings. Four replicates were performed at each station and repeated four times during June 2002 (Table 1).

Identification and data analyses.—All the spiders collected were preserved in 70% ethanol, transported to the laboratory for species identification and kept in the University collection (Rennes, France). In the tables, all means are presented with standard error (mean ± s.e.). Mean environmental and species variables were compared using ANOVA tests after verification of normal distribution according to Kolmogorov-Smirnov tests (MINITAB).

RESULTS

Comparison of habitat preference.—Catches by pitfall traps revealed that *Pardosa purbeckensis* activity abundances were significantly higher in natural than in invaded plots (Table 2). In accordance with trends found in activity, *P. purbeckensis* had a significantly higher density in natural plots. However, *Arctosa fulvolineata* had much higher densities in invaded than in natural plots, whereas its abundance did not differ significantly between the two vegetation types (Table 2).

Comparison of flooding effects between natural and invaded vegetation.—Based on their distribution change after the high tide, *Arctosa fulvolineata* and *Pardosa purbeckensis* presented similar reactions to flooding, with an unmodified distribution (in terms of presence/absence) in natural and invaded stations. Only *A. fulvolineata* almost disappeared from one natural station (level 2), where less than 5 individuals were caught after the high tide. In fact, this species presented comparable abundances before and after the high tide in invaded stations (Table 3), whereas its mean abundance significantly decreased in natural stations. *Pardosa purbeckensis* showed significantly decreased abundances after the high tide in invaded stations and constant abundances in natural stations (Table 3).

Comparison of habitat characteristics.—Invaded stations (*Elymus athericus*) differed significantly from natural stations (*Atriplex portulacoides*), i.e. they had deeper litter and taller plant cover (Table 4). No significant differences were found regarding soil salinity, soil water content and temperature. Regarding potential prey, Acari and Amphipoda (*Orchestia gammarella*) densities were significantly lower in invaded areas, leading to a decrease in total pedofauna at these stations (Table 4). No significant difference was found for Collembola.

Species from the guild of *Pardosa purbeckensis* (diurnal wanderers) were found in significantly higher densities in invaded than in natural stations (the more dominant species were the non-coastal *Pardosa prativaga*, *P. proxima* and *P. pullata*), whereas no difference between vegetation types was found for species from the *Arctosa fulvolineata* guild (nocturnal wanderers, mainly including the non-coastal *Agroeca lusatica*, *Clubiona stagnatilis* and *Zelotes latreillei*).

DISCUSSION

Changes in habitat characteristics after *Elymus* invasion.—Lycosids in general and the genus *Pardosa* in particular are known to prefer open habitats (e.g., Aart 1973), and Harvey et al. (2002) suggested that adults of *P. purbeckensis* are favored by low vegetation. Kessler & Slings (1980) demonstrated the tendency among juveniles of *P. purbeckensis* to aggregate and to select grass with high shoot densities, probably to avoid cannibalism. Because more diurnal wandering spiders are hunting in invaded plots, we suggest that young specimens of *P. purbeckensis* are exposed to a higher predation risk than in natural areas, contributing to the lower adult density in the invaded areas. Thus we propose that the habitat structure of *Elymus* (mainly tall vegetation and deep litter) was not suitable for this species and contributed to its lower occurrence in invaded habitats. In contrast, *Arctosa fulvolineata* might be favored by the structure of the invaded habitats: a deeper and more complex litter due to a lower rate of *Elymus* litter decomposition (Valéry et al. 2004). As a general rule, deep litter, by providing new microhabitats and microclimate conditions (Wise 1993), tends to favor nocturnal wanderers (case of *Arctosa fulvolineata*), ambush hunters (thomisids) and "litter–sensitive" sheet-weavers (Bell et al. 2001). Thus we suggest that *A. fulvolineata* prefers more heterogeneous litter of invaded areas, where it is often found during the day, at 3–4 cm depth (Pétillon pers. obs.).

Differences in the responses of dominant salt marsh species to the invasion can be influenced by many other factors than abiotic components of habitats. In particular for simple ecosystems such as salt marshes, interspecific competition may reduce spider populations (Schaefer 1972 according to Wise 1993; Marshall & Rypstra 1999). We propose that invaded habitats, by hosting other species from the same guild as *P. purbeckensis* (especially *Pardosa prativaga*, *P. proxima* and *P. pullata*), increased inter-specific competition. Contrary to *P. purbeckensis*, *A. fulvolineata* seemed not to be subjected to higher levels of competition in invaded habitats, as nocturnal wanderer densities were the same in natural and invaded habitats. Little is known about salt marsh spider diets, except predation upon Collembola for *P. purbeckensis* (Schaeffer 1974) and for the linyphiid *Erigone arctica* (White 1852) (Legel & Wingerden 1980). So, at the moment there is no evidence for food limitation, even if some potential prey decreased in invaded habitats (e.g., the amphipod *Orchestia gammarella*).

Changes in flood resistance in invaded habitats.—In this study, the two salt marsh species responded differently to flooding in invaded habitats. *Pardosa purbeckensis* abundances decreased only in invaded stations after the high tide. If this species uses underground refuges during flooding, as do several intertidal invertebrates (Foster & Treherne 1976; Kneib 1984), then it would be disfavored in invaded areas (deep but thin roots of *Elymus*) compared to natural areas (short and large roots of *Atriplex portulacoides*). Contrary to *P. purbeckensis*, *A. fulvolineata* seem to derive benefits from the invasive plant because its abundance remained the same after the high tide in the invaded stations and decreased in the natural stations. This litter-living species might be favored by *Elymus athericus* that seems to improve its habitat by increasing the food resources and the amount of air in the litter.

Conflicting aspects of the grass invasion: how to manage it.—Habitat suitability of natural and invaded areas clearly differed between the two wolf spiders. Activity trappability density of *P. purbeckensis* was strongly reduced in invaded areas indicating a decrease in the density and/or the mobility of individuals, whereas activity trappability density of *A. fulvolineata* was enhanced in invaded sta-

Table 4.—Habitat characteristics (mean ± s.e.) of natural and invaded stations, and statistical comparisons using ANOVA (Code: n.s. = non significant, * = $P < 0.05$, ** = $P < 0.01$).

	Units	Natural plots	Invaded plots	*F*-ratio	Code
Structural components					
Vegetation height	cm	29 ± 0.63	78 ± 1.64	331.43	**
Litter depth	cm	0	4 ± 0.23	754.60	**
Soil water content	%	60.13 ± 4.21	57.72 ± 1.12	0.31	n.s.
Soil salinity	mS/m	1009.7 ± 50.1	1013.8 ± 45.1	<0.01	n.s.
Soil diurnal temperature	°C	10.86 ± 0.62	11.00 ± 0.38	0.03	n.s.
Biotic components					
Amphipoda	Number/m^2	979 ± 311	205 ± 51	6.02	*
Acari	Number/m^2	55302 ± 8688	20202 ± 3085	14.49	**
Collembola	Number/m^2	5008 ± 2391	5645 ± 2574	0.03	n.s.
Total pedofauna	Number/m^2	60352 ± 7053	26293 ± 3707	18.27	**
Diurnal wanderers	Number/m^2	6.50 ± 2.10	29.25 ± 6.97	9.77	*
Nocturnal wanderers	Number/m^2	0.75 ± 0.48	5.25 ± 2.78	2.54	n.s.

tions. Here, quadrat results confirmed that changes in activity trappability densities also reflected changes in the species' population densities.

More than ten years after the grass invasion, the two dominant halophilic species are still present in invaded salt marshes (Fouillet 1986; present study). But our results indicate that in the near future microhabitat changes and (perhaps) competition for space and food between native and non-coastal (immigrated after the *Elymus* invasion) species could lead to a decline in the absolute density of the dominant native species such as *Pardosa purbeckensis*. This is a unique case of an invasion which involves, as it seems at the moment, both positive and negative aspects for dominant halophilic spiders, enhancing one species and reducing the other! As similar invasions are affecting more and more salt marshes in Western Europe (Bockelmann & Neuhaus 1999), we suggest that management plans should be undertaken for reducing the paradoxical consequences of *Elymus* invasion on typical and rare salt marsh biodiversity. The effects of mowing are surveyed at the moment in the Mont Saint-Michel bay. By re-opening the soil, mowing seems to maintain healthy populations of both halophilic species. This is in contrast to sheep-grazing that is likely to only favor *P. purbeckensis*, and even tends to disfavor both dominant halophilic wolf spiders when practiced in a too intensive way (Pétillon et al. submitted).

ACKNOWLEDGMENTS

We would like to thank P. Amaya Garcia, Q. Le Mouland, S. Michaud, G. Perrin, E. Pétillon and E. Villani for field assistance, Cobi Camberlein and Julien Cucherousset for English improvement. S. Toft and two anonymous reviewers greatly improved the manuscript by their remarks and suggestions. This study was supported by the French Ministry of Environment (Programme 'Espèces invasives') and the CNRS Zone Atelier 'La Baie du Mont Saint-Michel et ses bassins versants'.

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Manuscript received 29 December 2004, revised 7 September 2005.